Anatomy of the Foregut of *Morum* Röding, 1798 (Gastropoda: Tonnacea) and the Taxonomic Misplacement of the Genus

by

ROGER N. HUGHES

School of Animal Biology, University College of North Wales, Bangor, Gwynedd, LL57 2UW, U.K.

Abstract. Dissections and serial sections reveal that *Morum* differs anatomically from cassids in the following ways. There is a pair of large, acinar salivary glands that are mingled into a compact mass, but no proboscis glands. The salivary ducts do not run through the nerve ring, but become embedded in the oesophageal wall anterior to it. The proboscis sheath is capable of complete introversion and the oesophagus is attached to it, so being thrown into a Z-bend when the proboscis retracts. There are no jaws. The buccal mass and radula are microscopic. The radula has one tricuspid tooth (rachidian) per row. The mid-oesophageal epithelium is extensively folded longitudinally, not forming the distinct, transversely pleated oesophageal gland of cassids. The position of the salivary ducts anterior to the nerve ring, the lack of jaws, the reduced radula, and the arrangement of the introverted proboscis are features typical of neogastropods rather than mesogastropods. The large propodial shield, long siphon, ability to autotomize the hind-foot, microscopic radula with single tricuspid tooth per row, wide mid-oesophagus with longitudinal pleats, absence of accessory salivary, and Leiblein's and anal glands indicate that *Morum* belongs to the Harpidae.

INTRODUCTION

Morum is placed in the tonnacean family Cassidae (ABBOTT, 1968; EMERSON, 1981), yet several characteristics set this genus apart from the other cassids. The shell (Figure 1A) has some marked dissimilarities: "The anterior end of the aperture looks as though it had been broken, because it lacks the turned-back edge of most related forms. The young shell has even been mistaken for a cone by unsuspecting collectors" (KEEN & McLEAN, 1971). These authors described the shell of *Morum veleroae* Emerson, 1968, as "looking like a cross between a stromb and a harp shell . . . ." The egg capsules, rather than being simple tubular or flask-shaped structures as in other cassids (ABBOTT, 1968; D'ASARO, 1969; BANDEL, 1976; HUGHES, 1985), are knobby, discoidal, and stacked in a row on a basal membrane, resembling certain *Conus* capsules (WORK, 1969; BANDEL, 1976). The active animal has a propodial shield, a long siphon, long cephalic tentacles, and rapid movement quite unlike other cassids (present observations). Moreover, whereas other cassids are specialized consumers of echinoids (HUGHES & HUGHES, 1981; DU SHANE, 1982; HUGHES, 1985), *Mo-rum oniscus* (Linnaeus, 1767), the only species to be experimentally observed alive, refused all types of echinoderms offered to it (WORK, 1969; present observations) and no conclusive evidence of its diet is available.

The present paper describes the anatomy of the foregut of *Morum tuberculosum* (Reeve, 1842), confirming not only the gross dissimilarity of *Morum* from other cassid genera, but also that it belongs to the Neogastropoda.

MATERIALS AND METHODS

Morum oniscus was sought by intensive scrutiny of the reef flat near the Smithsonian Tropical Research Institute's (STRI) Caribbean laboratory at Galeta Point, Republic of Panama. Despite over a week of continued effort, only one specimen was found, although several sets of egg capsules were seen. The specimen, collected at night beneath a slab of reef rock overlying coarse sand, was observed for 2 wk in the aquarium of the Pacific laboratory of STRI on Naos Island, Republic of Panama. Coelenterates, polychaetes, mollusks, crustaceans, and fish, both alive, freshly killed and decomposing, were offered as food, but none was eaten. The specimen was fixed and dissected.
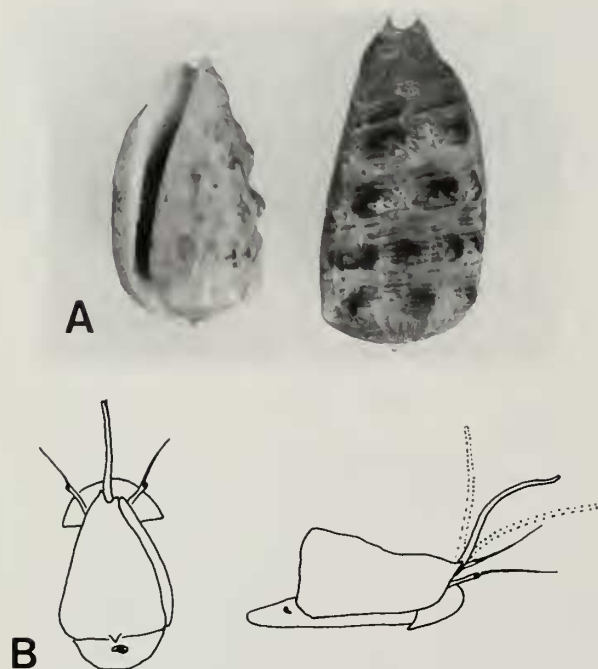
Figure 1

A. *Morum tuberculosum*. Shell length, 34 and 28 mm. B. *Morum oniscus,* showing appearance of the propodial shield, siphon, and cephalic tentacles when the snail is moving over the substratum. Shell length, 15 mm.

Searches for the Pacific species *Morum tuberculosum* on all types of shore within 10 km of the Naos laboratory were unproductive. Six intact, fixed specimens, 10–32 mm in shell length, were kindly sent at a later date by Royce E. Hubert, who had collected them under rocks and in areas of muddy sand at low tide at night on 28 February 1983. One specimen is lodged with the British Museum of Natural History, registration No. 1985118. The smallest specimen was serially sectioned at a thickness of 8 μm per section and stained with Mallory triple stain. The rest were dissected under a low-power binocular microscope. The radula was prepared by macerating the tip of the proboscis in hot, 10% sodium-hydroxide solution until almost dry (2 h) and transferring the proboscis to a drop of water on a microscope slide attached to an EM stub, whereupon the tissue dissolved leaving the microscopic radula intact. Sodium hydroxide was removed by rinsing with freshwater using a micro-pipette. A small hair from the back of the hand was dipped in cellotape glue (obtained by immersing the adhesive tape in trichloroethylene) and used to secure the radula to the coverslip. After coating with gold, but without prior sonication, the radula was examined using a scanning electron microscope. Attempts to locate the radula by clearing the proboscis in cedarwood oil or in lactophenol and lignin pink failed

because the radula is too small to be seen *in situ* under the low power of a dissecting microscope.

RESULTS

Morum oniscus

The *Morum oniscus* burrowed rapidly into the sand when illuminated by torchlight on the reef flat. In the aquarium it remained buried beneath the sand during daylight, the siphon communicating with the surface. On some nights the specimen emerged to glide over the substratum, turning erratically along its path. The impression given was of a more agile snail than the typical cassid. The propodium formed a pronounced semicircular shield; the siphon was held at various angles, extending far beyond the siphonal canal, and the cephalic tentacles were also greatly extended (Figure 1B). The animal quickly burrowed in response to any kind of disturbance and would not feed, even when undisturbed for a week. Anatomical features of the *M. oniscus* were similar to those of *M. tuberculosum* described below.

Morum tuberculosum

The siphon opens onto the tip of a large, bipectinate osphradium (Figure 2A). The gill is also large and the hypobranchial gland is well developed, producing copious amounts of mucus but no colored secretion.

On removing the dorsal wall of the cephalic hemocoel, the introverted proboscis sheath lies to the right and the solid, white salivary glandular mass to the left, occupying most of the available space (Figures 2A, 3A). The proboscis sheath is attached to the body wall by numerous short, fine muscle strands near the rhynchostome and by a series of large, straplike retractor muscles further along its length (Figure 3B). The fully retracted proboscis lies, sometimes bent into folds, within the completely introverted proboscis sheath (Figure 4B).

The anterior oesophagus emerges from the base of the introverted proboscis sheath and runs back on itself to the midway position, closely attached to the proboscis sheath by a short mesentery (Figure 4A). Here the anterior oesophagus bends posteriorly and, along with the aorta, passes as a narrow tube through the massively concentrated nerve ring (Figure 5). On emerging posteriorly from the nerve ring, the oesophagus dilates to form a wide, internally pleated mid-oesophagus that runs to the left, passing beneath the posterior salivary gland (Figure 5). The mid-oesophagus continues, without clear differentiation, into the narrower posterior oesophagus, running to the left until it merges with the simple stomach (Figures 2B, C), which lies on the opposite side of the animal, level with the nerve ring.

The salivary glands form a dense, irregularly shaped mass in which the two glands are indistinguishable. The shape and relative size of the glandular mass varies among
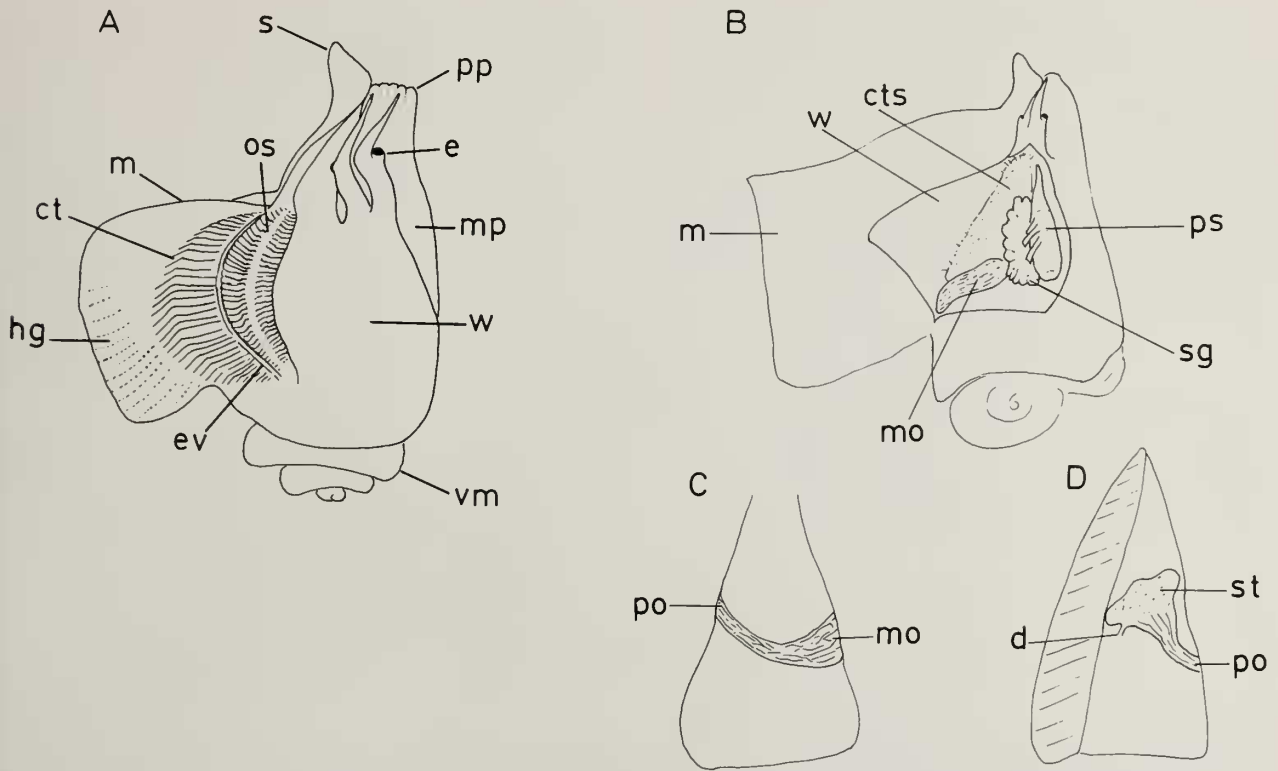
Figure 2

Morum tuberculosum, body about 20 mm long. A. The mantle is peeled to the left, showing the arrangement of the pallial organs. B. The dorsal wall of the cephalic hemocoel has been peeled to the left, revealing the natural positions of the retracted proboscis, mid-oesophagus, and salivary glands. C. The mid-oesophagus traced to the left where it merges with the posterior oesophagus. D. The posterior oesophagus traced further to the left where it joins the stomach. The hatched region shows where the foot has been cut away. ct = ctenidium; cts = connective tissue; d = digestive gland duct; e = eye; ev = efferent branchial vessel; hg = hypobranchial gland; m = mantle; mo = mid-oesophagus; mp = mesopodium; os = osphradium; po = posterior oesophagus; pp = propodium; ps = proboscis sheath; s = siphon; sg = salivary gland; st = stomach; vm = visceral mass; w = wall of cephalic hemocoel.

animals (Figures 2B, 3A, B), but is always large. Especially in specimens with smaller salivary glands, the unoccupied space on the left side of the cephalic hemocoel is filled with a gray, semi-translucent, spongy material that has no ducts and appears to be a form of connective tissue. It is closely applied to the body walls and is traversed by several large nerves and by numerous fine muscle strands.

One salivary duct serves the posterior region of the glandular mass and the other empties from the anterior region (Figure 8E). The salivary ducts become embedded lateroventrally in the anterior oesophagus where it bends away from the proboscis sheath and, therefore, they do not pass through the nerve ring (Figure 5). There is no accessory salivary gland.

The buccal mass (Figure 7) lies at the tip of the proboscis. It is supported by a pair of minute odontophoral cartilages that unite anteriorly to form a grooved boss over

which the radula runs in the normal way (Figures 7B, C). The radula itself is microscopic, about 25 μm wide in a large specimen, consisting of a single column of tricuspid teeth (Figure 6).

There is a pronounced median dorsal fold projecting down from the roof of the buccal cavity and it continues in a less pronounced form along the anterior oesophagus (Figure 8E) to the level of the nerve ring, whereupon it disappears. Behind the level where the odontophore projects into the buccal cavity, a median ventral fold projects upwards, abutting the dorsal fold and so dividing the oesophageal lumen into two lateral cavities (Figures 7B, C). Like the dorsal fold, the ventral fold disappears just before the oesophagus enters the nerve ring.

The salivary ducts open onto lateral papillae immediately in front of the buccal mass (Figures 7A, B). Throughout their length, the salivary ducts are equipped
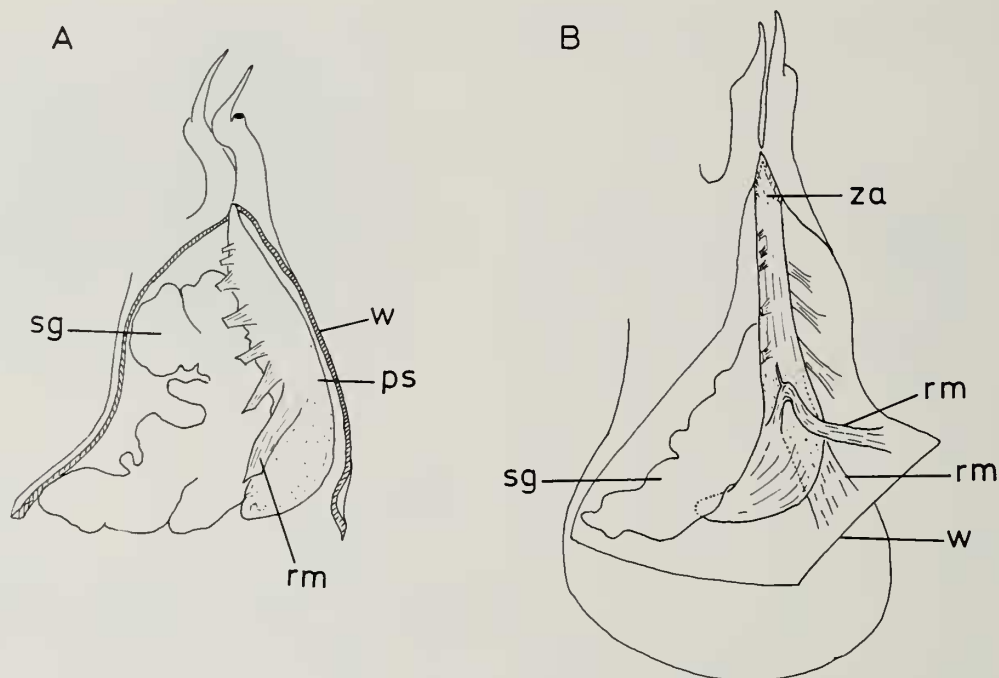
Figure 3

Morum tuberculosum. A. Details of the retracted proboscis and salivary glands. The latter are more extensive and shaped differently from the specimens in Figures 2B, 3B. B. Retracted proboscis, showing insertions of the retractor muscles on the wall of the cephalic hemocoel. ps = proboscis sheath; rm = retractor muscle; sg = salivary gland; w = wall of cephalic hemocoel; za = zone of attachment of proboscis sheath to body wall.
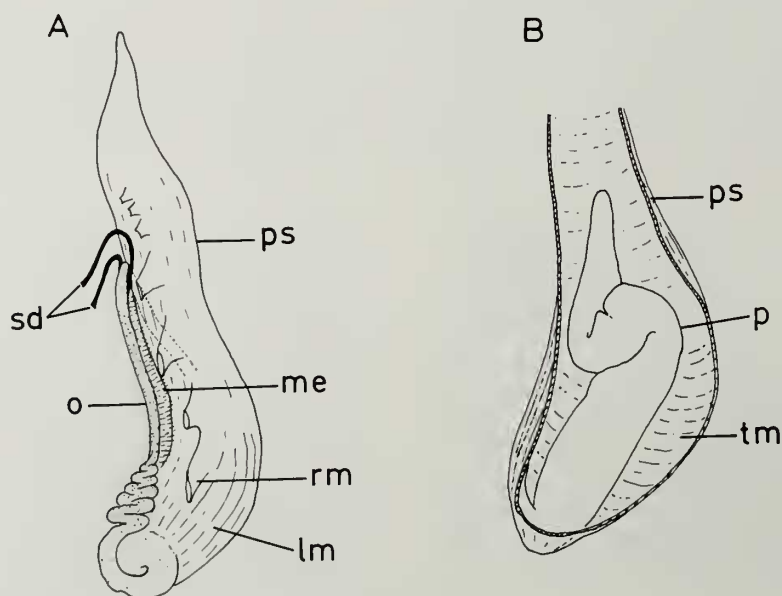
Figure 4

Morum tuberculosum. Details of retracted proboscis. A. Attachment of salivary ducts and anterior oesophagus to the proboscis sheath. B. Proboscis retracted and folded within the proboscis sheath. lm = longitudinal muscles of proboscis sheath; me = mesentery attaching oesophagus to proboscis sheath; o = oesophagus; p = proboscis; ps = proboscis sheath; rm = retractor muscle; sd = salivary duct; tm = transverse muscle of proboscis sheath.
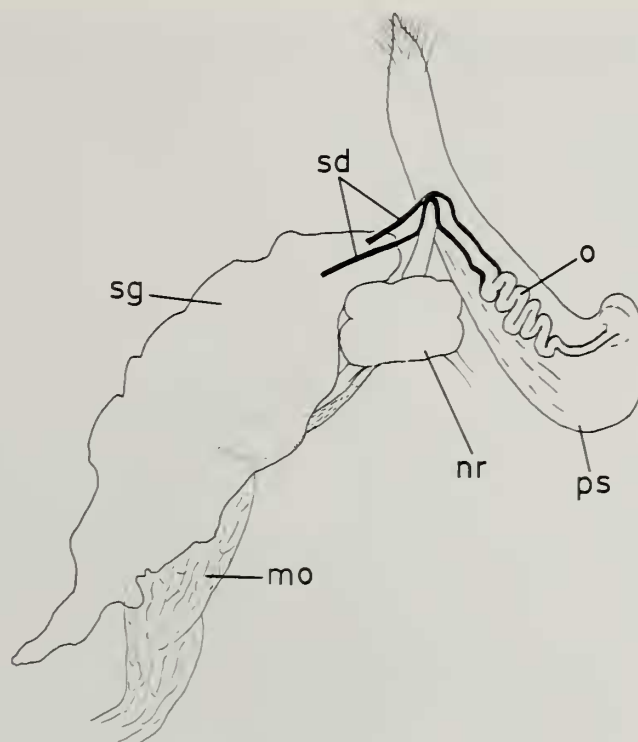
Figure 5

Morum tuberculosum. Passage of the oesophagus from the proboscis sheath through the nerve ring. mo = mid-oesophagus; nr = nerve ring; o = anterior oesophagus; ps = proboscis sheath; sd = salivary ducts; sg = salivary glands.

with strongly developed circular muscles (Figures 7, 8E). Ramifications of the salivary ducts can be traced within the salivary glands, which themselves are made up of small, closely packed acini comprised of cells densely populated by granules.

As it passes through the nerve ring, the oesophagus becomes narrow and lined by a simple epithelium without folds (Figure 8C). The wide, mid-oesophagus is lined by an extensively folded epithelium that is arranged predominantly into longitudinal pleats, but also with some transverse folds (Figures 8D, F). The posterior oesophagus is narrower, but with similar epithelial folds. The stomach is lined by similar, but larger folds. The rectum lacks an anal gland.

DISCUSSION

The alimentary anatomy of *Morum* is grossly dissimilar from that of other cassids, as may be seen by comparing Figures 2–5 with the dissection of *Phalium granulatum* (Born, 1778) (Figure 9) or with figure 1a of HUGHES & HUGHES (1981). *Morum* has a pair of dense salivary glands fused into a large mass; cassids have a distinct pair of small acinar salivary glands and a pair of huge, spongy proboscis glands. The salivary ducts of *Morum* join the

oesophagus anterior to the nerve ring and are deeply embedded in the oesophageal wall; the salivary ducts of cassids pass through the nerve ring and are not deeply embedded in the oesophageal wall. The proboscis of *Morum* can be retracted far within the proboscis sheath; the proboscis of cassids does not retract much within the level of the rhynchostome. The proboscis sheath of *Morum* is withdrawn by a few, long retractor muscles that effect complete introversion; the proboscis sheath of cassids is withdrawn by numerous shorter retractor muscles and introversion is never complete even when the proboscis is fully retracted. The middle section of the anterior oesophagus of *Morum* is attached to the proboscis sheath by a short mesentery, with the result that on retraction of the proboscis and introversion of the proboscis sheath, the anterior oesophagus is thrown into a Z-bend; the anterior oesophagus of cassids lies freely within the lumen of the proboscis sheath and remains straight when the proboscis sheath is withdrawn. The mid-oesophagus of *Morum* is lined by a predominantly longitudinally folded epithelium and passes without clear demarcation into the narrower posterior oesophagus; the mid-oesophagus of cassids forms a distinct oesophageal gland with a transversely pleated epithelium. The buccal mass and radula of *Morum* are
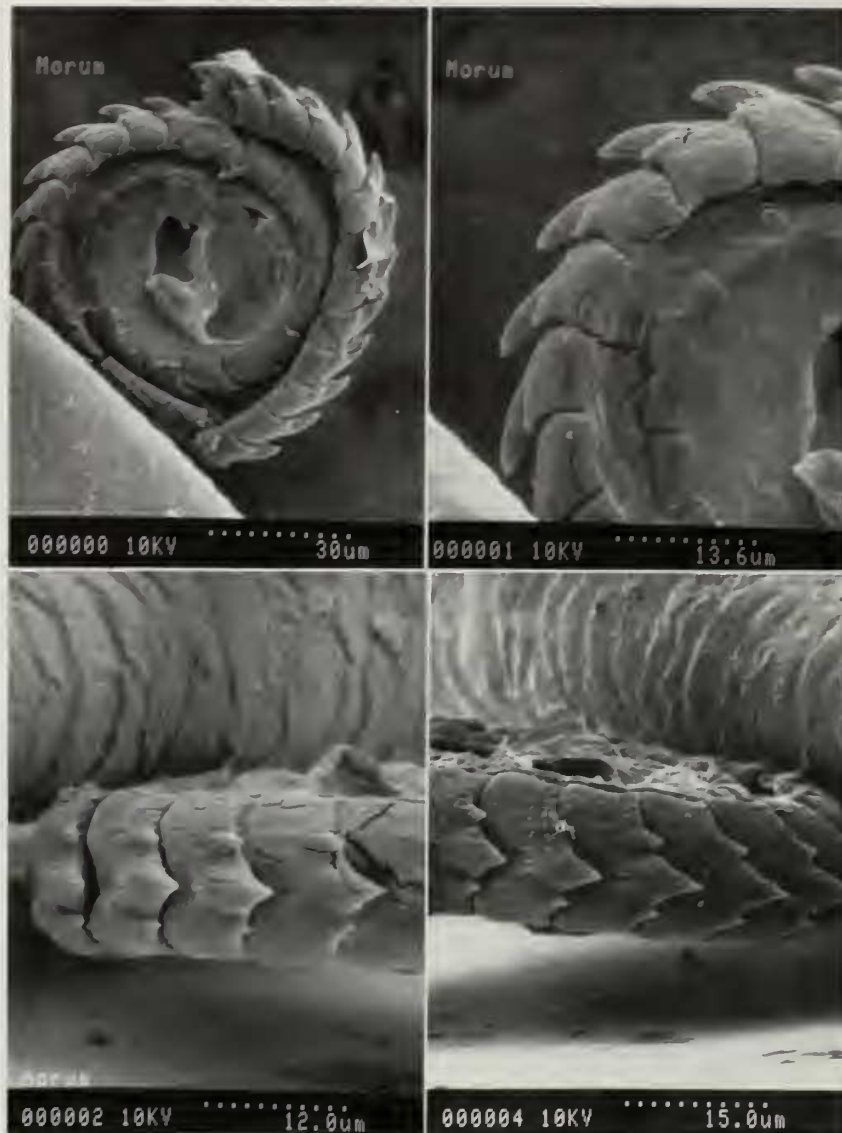
Figure 6

Morum tuberculosum. Scanning electron micrographs of the radula, taken from a specimen with a shell length of 25 mm.

microscopic and the radula has only one tooth per row; the buccal mass and radula of cassids are of normal proportions and the radula has seven teeth per row. The central tooth of *Morum* is tricuspid; the central tooth of cassids has many cusps. *Morum* lacks jaws; cassids have a pair of lateral jaws.

There are other morphological differences between *Morum* and cassids. The propodium of *Morum* forms a semicircular shield, but there is no suggestion of a propodial shield in cassids. The siphon of *Morum* extends far beyond the siphonal canal, but does not do so in cassids.

Morum appears to be trophically distinct from the cassids. The refusal of echinoid prey, the structure of the buccal apparatus, and the absence of acid-secreting proboscis glands show that *Morum* could not drill echinoid tests in the manner that is characteristic of cassids (HUGHES & HUGHES, 1981).

Together, these facts indicate that *Morum* does not belong to the Cassidae, nor even to the Tonnacea, all of which have paired salivary and acid-secreting proboscis glands, salivary ducts running through the nerve ring, and a distinct oesophageal gland (HUGHES & HUGHES, 1981). In-
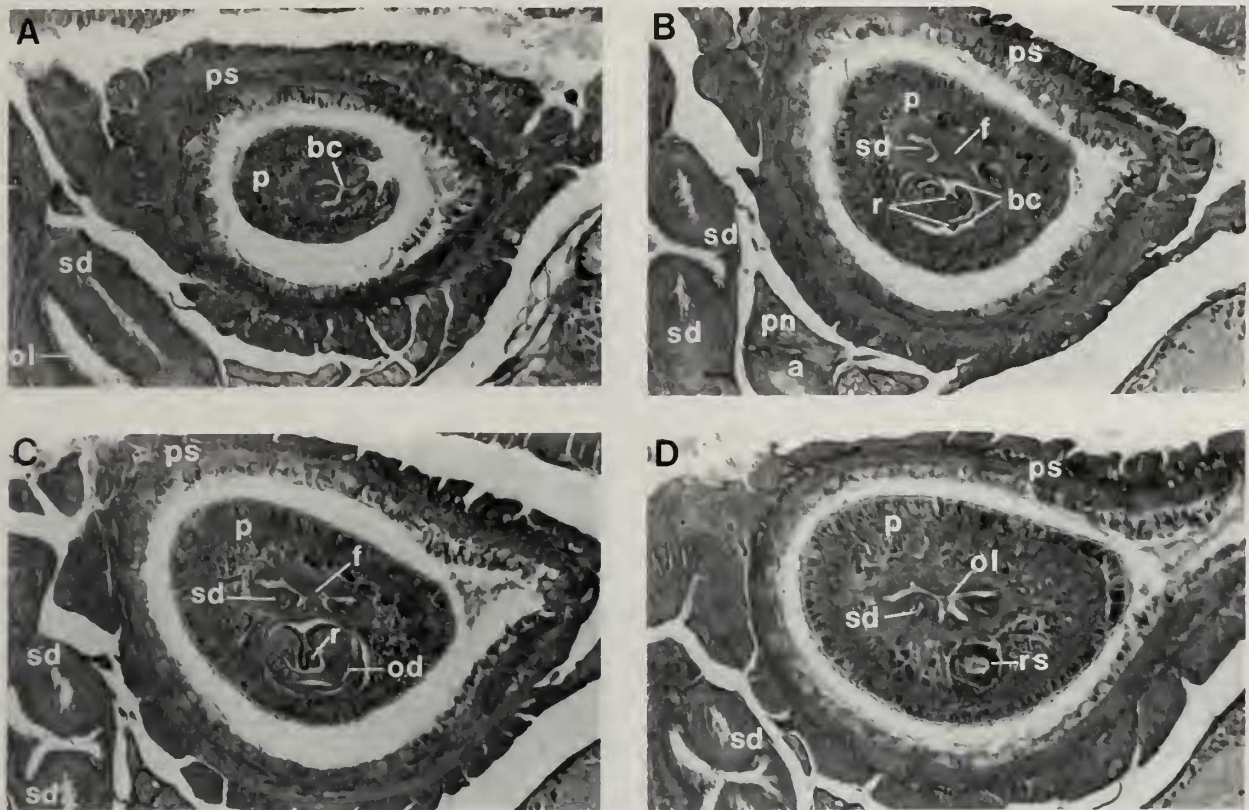
Figure 7

Morum tuberculosum. Transverse sections through the buccal apparatus. Magnification, ×187. A. Immediately anterior to the tip of the odontophore; the salivary ducts have emptied into the buccal cavity slightly posterior to this section. B. The tip of the odontophore; the radula runs over both the dorsal and ventral surface of the odontophore; the salivary ducts are about to open via the ventrolateral papillae into the buccal cavity; mid-dorsal and mid-ventral folds of the oesophageal epithelium meet. C. Further behind the tip of the odontophore; the radula lies within a deep groove; the radular membrane lines the walls of the groove; the small, paired odontophoral cartilages are visible. D. Behind the odontophore; the radular sac is visible; the dorsal and ventral oesophageal folds are less prominent and do not meet. For legend see Figure 8.

deed, the position of the salivary ducts anterior to the nerve ring reveals that *Morum* has closer affinities with the Neogastropoda (PONDER, 1973) than with the Mesogastropoda, to which cassids belong. *Morum* is consistent with all other neogastropods in lacking jaws (PONDER, 1973) and shares several other features with various neogastropod families.

The mode of introversion of the proboscis sheath, the attachment of the oesophagus to the wall of the proboscis sheath, and the Z-bend of the oesophagus produced by its retraction are similar to the case with *Nassarius* (FRETTER & GRAHAM, 1962:fig. 115). A microscopic buccal apparatus is found also in some members of the Colubrariidae, Harpidae, Muricidae, and Columbariidae (PONDER, 1973). Reduction of the radula tooth row to the rachidian occurs also in the Mitridae, Volutidae, Marginellidae, Volutomitridae, and Cancellariidae, but the tricuspid cen-

tral tooth of *Morum* bears closer resemblance to that of *Harpa* (see PONDER, 1973) than to that of other genera. A long siphon extending beyond the siphonal canal is found among numerous neogastropods, notably nassariids, but also among some mesogastropods. A propodial shield is found in the Harpidae and Olividae (PONDER, 1973). The absences of a valve of Leiblein and a gland of Leiblein in *Morum* are features shared by a number of neogastropod families (PONDER, 1973). The absence of paired dorsal folds in the anterior oesophagus precludes identification of the site of torsion.

Morum bears closest resemblance, however, to the Harpidae (W. Emerson and W. Ponder, personal communications); common features include the propodial shield, long siphon, ability to autotomize the hind-tip of the foot (A. Connell and W. Liltved, personal communications), microscopic radula and single tricuspid tooth per row
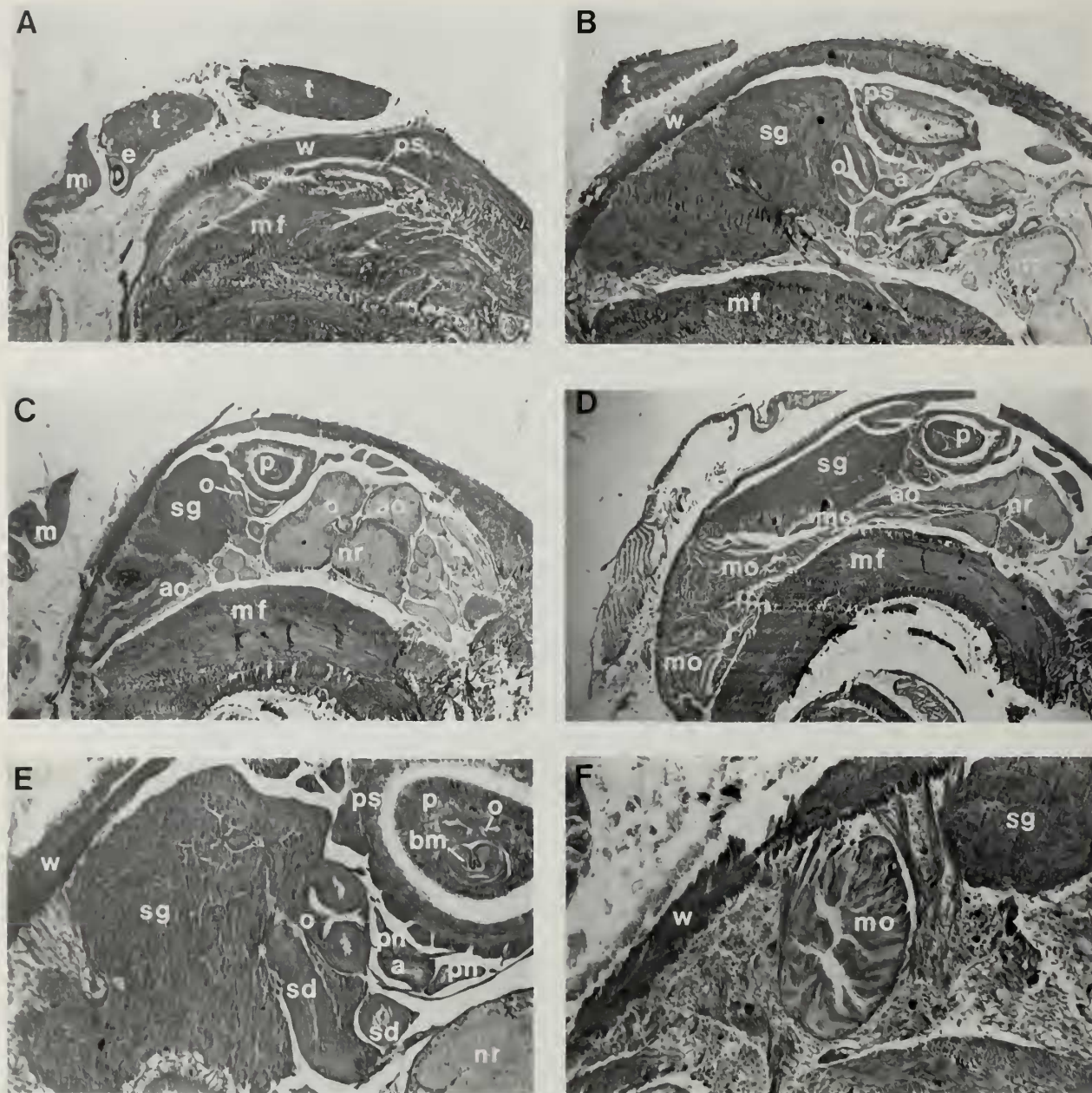
Figure 8

Morum tuberculosum. A. The tip of the proboscis sheath, close to the rhynchostome; magnification, ×28. B. The anterior oesophagus entering the nerve ring; magnification, ×37. C. The anterior oesophagus within the nerve ring; magnification, ×28. D. The oesophagus emerging posteriorly from the nerve ring and widening into the mid-oesophagus; magnification, ×28. E. One salivary duct, sectioned obliquely, is entering the anterior salivary gland, the other, sectioned transversely, serves the posterior salivary gland. The anterior oesophagus is seen with a pair of muscular salivary ducts embedded in its wall and with small dorsal and ventral folds projecting into its lumen. The oesophagus, together with the proboscis artery and proboscis nerves, is connected to the proboscis sheath by a mesentery; magnification, ×93. F. The mid-oesophagus showing the extensively folded epithelium; magnification, ×93. a = proboscis artery; ao = aorta; bc = buccal cavity; bm = buccal mass; e = eye; f = dorsal and ventral folds; m = mantle; mf = muscular floor of cephalic hemocoel; mo = mid-oesophagus; nr = nerve ring; o = anterior oesophagus; od = odontophore; ol = oesophageal lumen; p = proboscis; pn = proboscis nerve; ps = proboscis sheath; r = radula; rs = radular sac; sd = salivary duct; sg = salivary gland; t = cephalic tentacle; w = wall of cephalic hemocoel.
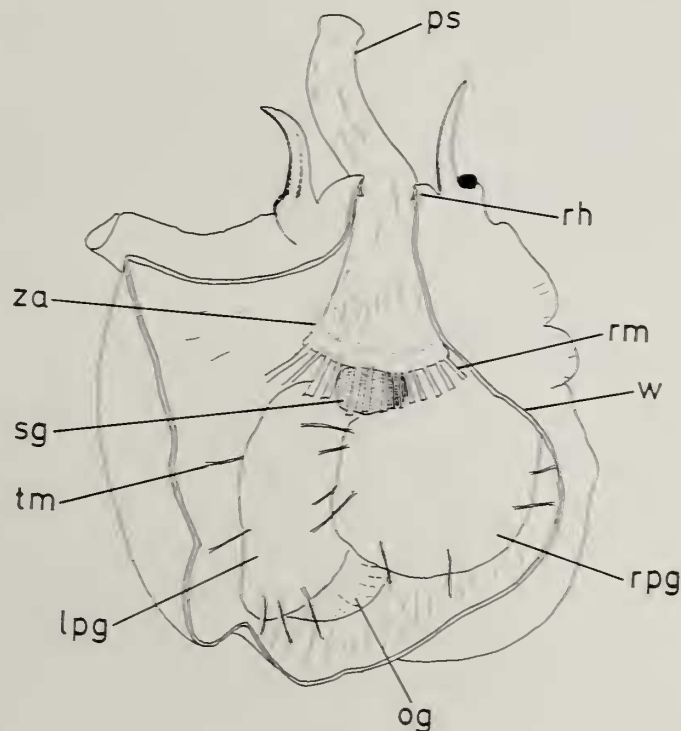
Figure 9

Phalium granulatum, showing arrangement of the partially invaginated proboscis sheath with its numerous retractor muscles, the massive proboscis glands, the small salivary glands (only one visible), and the oesophageal gland; for comparison with the foregut anatomy of *Morum tuberculosum*. lpg = left proboscis gland; og = oesophageal gland; ps = proboscis sheath; rh = rhynchostome; rm = retractor muscle; rpg = right proboscis gland; sg = salivary gland; tm = tie-muscle; w = wall of cephalic hemocoel; za = zone of attachment of proboscis sheath to body wall.

(REHDER, 1973), and lack of accessory salivary, Leiblein's and anal glands (W. Ponder, personal communication; personal observation). Preliminary dissections leave no doubt that *Morum* belongs to the Harpidae and a detailed comparison together with a taxonomic revision are underway (Hughes & Emerson, in preparation).

The feeding habits of *Morum* remain enigmatic but perhaps, like those of *Harpa* (REHDER, 1973), they involve the capture of crustaceans, using the large propodium and copious secretion of sticky mucus to envelop the prey. Certainly, *Morum* is sufficiently agile for this method of attack. The large salivary glands with their densely granular cells, together with the highly muscular salivary ducts, suggest that digestively active saliva is ejected from the proboscis. Perhaps food is ingested as a partially digested fluid. This would pass easily through the narrow part of the oesophagus at the nerve ring and would require minimal processing before entering the stomach, hence the absence of a gland of Leiblein. Fine muscle strands connecting the wide mid-oesophagus to the body wall, especially evident in *Harpa* (personal observation), indicate that this section of the gut may serve as a dilatable pump for the ingestion of fluid. The microscopic radula would suffice to penetrate the thin arthrodial membranes of the crustacean prey, allowing the injection of saliva and withdrawal of semidigested fluid.

LITERATURE CITED

ABBOTT, R. T. 1968. Helmet shells of the world (Cassidae): 1. Indo-Pacific Mollusca 2:7-201.

BANDEL, K. 1976. Die Gelege karibischer Vertreter aus den Uberfamilien Strombacea, Naticacea und Tonnacea (Meso-

gastropoda) sowie Beobachtungen im Meer und Aquarium. Mitt. Inst. Colombo-Aleman Invest. Cient. 8:105–139.

D'ASARO, C. N. 1969. The spawn of the emperor helmet shell, *Cassis madagascariensis* Lamarck, from south Florida. Bull. Mar. Sci. 19:905–909.

DU SHANE, H. 1982. Notes on living *Casmaria vibexmexicana* (Stearns, 1894). Veliger 24:336–338.

EMERSON, W. K. 1981. Two new Indo-Pacific species of *Morum* (Gastropoda: Tonnacea). Nautilus 95:101–105.

FRETTER, V. & A. GRAHAM. 1962. British prosobranch molluscs: their functional anatomy and ecology. The Ray Society: London. 755 pp.

HUGHES, R. N. 1985. Laboratory observations on the feeding behaviour, reproduction and morphology of *Galeodea echinophora* (Gastropoda: Cassidae). Zool. J. Linn. Soc. 86:355–365.

HUGHES, R. N. & H. P. I. HUGHES. 1981. Morphological and behavioural aspects of feeding in the Cassidae (Tonnacea, Mesogastropoda). Malacologia 29:385–402.

KEEN, A. M. & J. H. McLEAN. 1971. Sea shells of tropical west America: marine mollusks from Baja California to Peru. 2nd ed. Stanford University Press: Stanford. 1064 pp.

PONDER, W. F. 1973. The origin and evolution of the Neogastropoda. Malacologia 12:295–338.

REHDER, H. A. 1973. The family Harpidae of the world. Indo-Pacific Mollusca 3:207–221.

WORK, R. C. 1969. Systematics, ecology and distribution of the mollusks of Los Roques, Venezuela. Bull. Mar. Sci. 19:614–711.